GRAVITY AS A FORM-STIMULUS IN FUNGI

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY
XCII

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(WITH THREE FIGURES)

The directive influence of gravity in determining the position of the hymenium in the higher Basidiomycetes is a matter of common observation. The fruit-bodies of these fungi are universally oriented so that the hymenium is exposed toward the earth's surface. If the normal position of the fruit-body is changed, either by accident or by experimentation, readjustment takes place by which the hymenial surface is again brought into a horizontal plane, provided of course that such readjustment is not hindered by other factors. Interesting cases illustrating these phenomena are given by ATKINSON[1] and also by WATERS.[2]

The methods by which the horizontal orientation of the pileus is brought about are two. First, in all stalked forms, such as the Agaricaceae, and some of the Polyporaceae and Hydnaceae, the stalks are negatively geotropic, and by their curvature always bring the pileus into a horizontal position. This property was first observed by HOFMEISTER[3] in some of the Agaricaceae. The phenomena may be observed in all stalked forms growing on the sides of trees or stumps. Here the stems curve upward until the pileus is brought into the normal position. Second, in forms which have no stalk, and this applies especially to sessile forms of Polyporaceae, the orientation of the hymenium is brought about by the growth of the trama-plates themselves, for, as SACHS[4] has shown, the trama-plates of the hymeno-

[1] ATKINSON, G. F., Mushrooms, edible, poisonous, etc. pp. 13–17. 1900.
————, Some wood-destroying Fungi. Geol. Surv. of Louisiana, Rep. 1899: 333–338. *pls.* 7.

[2] WATERS, C. E., Geotropism of Polyporus. Plant World **7**:224. 1904.

[3] HOFMEISTER, W., Ueber die durch die Schwerkraft bestimmten Richtungen von Pflanzentheilen. Jahrb. Wiss. Bot. **3**:92. 1863.

[4] SACHS J., Experimental Physiologie. p. 93. 1865.

phore, not only in the Polyporaceae but also in the Hydnaceae and Agaricaceae, are positively geotropic. Since in non-stalked forms adjustment of the whole pileus is obviously impossible, the downward growth of the hymenophore alone is responsible for the orientation of the hymenium. If the position of the growing pileus is changed, readjustment to the new condition is accomplished solely by the change in direction of growth of the elements of the trama-plates and the growing, undifferentiated elements of the pileus. This often results in the formation of new pilei growing at various angles from the old pileus (see ATKINSON, *l. c.*).

In such types as the Polyporaceae it is evident that the form of the fungus depends to a large extent on the growth of the trama-plates making up the hymenophore. Since the mode of growth of these elements is greatly influenced by gravity, the question naturally arises as to what extent the form which these fungi assume is determined by the responses of the elements to the influence of gravity. To determine the effect of gravity as a form-stimulus, klinostat experiments were conducted with a number of fungi from different families. As a rule sticks and branches upon which sporophores were growing were brought into the laboratory for experimentation. Although a considerable number of plants were thus tried, only a few gave results, owing, no doubt, to the fact that the conditions of growth of these forms are not sufficiently well understood so that they can be cultivated with certainty. From a few forms interesting results were nevertheless obtained. The experiments are here first described, and this is followed by a discussion of the significance of the results obtained.

In October 1905 a small fruit-body of *Polystictus cinnabarinus* growing on a stick was placed in a moist chamber and rotated on the horizontal axis of the klinostat until the middle of December. The fruit-body was a little over 1^{cm} in diameter, with few pores, and growing at the margin. During the experiment its growth was slow, although the plant appeared to remain healthy. At the end of the experiment the plant was about 2^{cm} in diameter. The new growth, however, was not confined to the margin as in stationary fruit-bodies, but owing, no doubt, to the still embryonic condition of the fruit-body growth was resumed over the entire surface, resulting

in a pulvinate fruit-body. The most remarkable result of the experiment, however, is this: the fruit-body was no longer differentiated into a sterile dorsal and fertile ventral surface; the whole pulvinate body was covered with tubes characteristic of the hymenial surface of this fungus. At the present time it is scarcely possible to distinguish the original dorsal and ventral surfaces of the specimen, which has been preserved in alcohol. With the suspension of the differentiation of dorsal and ventral surfaces, all tendency of the fruit-body to produce the normal shelf-like form is of course lost.

On October 9, 1906, a stick with several growing fruit-bodies of *P. cinnabarinus* was placed in a moist chamber as before, and revolved in a dark chamber until December 15. At the same time several other sticks with growing fruit-bodies were similarly arranged and revolved, without excluding the light. Of all the fruit-bodies used in this experiment only one rather large specimen in the dark chamber showed any uniform growth.[5] This one had grown on the upper side of a dead branch, so that it had a somewhat rotate form, attached at the center. The sporophore was about 3.5^{cm} in diameter. The growth of this plant on the klinostat was extremely slow, so that it did not enlarge much. New growth occured along a zone on the margin, extending back for about 1^{cm} over the dorsal surface. The result was a tumid thickening of the otherwise somewhat acute margin of the pileus. Here again the whole growing zone showed the incepts of numerous pores characteristic of the hymenial surface. That these were not more developed, as in the former case, is due to the unfavorable conditions of growth, for it should be remembered that the other fruit-bodies used in this experiment, whether growing in light or darkness, made scarcely any growth at all, although they remained fresh and normal to all appearances.

Among the Agaricaceae experiments were carried out with *Schizophyllum commune* and some species of Coprinus.

Pieces of a maple branch containing mycelium of Schizophyllum were placed on the klinostat as in former experiments. At the beginning of the experiment any traces of sporophores visible on the

[5] At the end of the experiment it was found that several of the smaller fruit-bodies had developed well-marked pores in patches, where growth had been resumed on the margin and on the upper surface.

branch were removed. It was therefore certain that if any fruit-bodies appeared, they had developed from their earliest stages on the klinostat. The precaution is important, since the fruit-bodies of the Agaricaceae are completely differentiated during their earliest stages of growth. Beyond these stages the parts, therefore, can no longer be subject to formative stimuli. On several of these sticks the fruit-bodies developed within about a month. They appear as small outgrowths resembling simple forms of Clavaria, and attain a length of about 1^{cm}. Early in their development a cup-like depression appears at the summit, and within this the rudimentary lamellae are formed, radiating from the center. The fruit-bodies at this stage have the form of a short trumpet about 1^{cm} long. The outside has the characteristic appearance of the dorsal surface of the normal fruit-body. By subsequent growth the margin expands uniformly at first, but later unequally, so that the resulting fruit-body is a lobed disk, $2–3^{cm}$ in diameter, and stalked at the back. The curious fact brought out by this experiment is that the lamellae develop on the inner side of the trumpet- or funnel-shaped fruit-body. The pileus, therefore, appears to be attached at the back, with the lamellae developing on the morphologically upper side.

To study the effect of gravity on some more specialized form, dung-cultures were set up for Coprinus. These were continually rotated so that the entire development of the fungi from the germination of the spore to the maturation of the fruit-body took place on the klinostat. The primordia of the fruit-bodies were thus at no time subject to the normal influence of gravity. Several crops of Coprinus developed on the cultures, but the fruit-bodies were normal in every way. Their direction of growth was perpendicular to the substratum, the actual direction being horizontal, since the pots were rotated on the horizontal axis of the klinostat.

The experiments with the foregoing three types show the existence of a marked difference in the degree to which the form of these types is modified by or depends upon the stimulus of gravity. Of the plants studied, Polystictus is the more plastic, and is consequently more influenced by gravity. Here the differentiation of the fruit-body into the sterile dorsal and fertile ventral surface depends on the direct or indirect action of gravity. In Schizophyllum the tissue

differentiation is independent of the external stimulus of gravity, but the general form of the plant is somewhat modified in a way to be considered later. In the highly differentiated Coprinus the morphogenic influence of gravity is not evident.

The sporophores of all the higher fungi are made up of a complex mass of hyphae whose growth is so correlated that the final result is the definitely organized fruit-body. These hyphae must be considered to a large extent as independent individuals, for they have organic connection only in so far as they arise from common branches many cell generations back in the tissue, or in so far as they are united by subsequent fusion which is comparatively rare. The elements, nevertheless, grow in unison to form the sporophore. As the organization of the sporophore is in the main the result of successive changes in the direction of growth of elements,[6] it seemed possible that this mode of growth might be determined by external stimuli, coupled of course with a changing capacity of the elements for reacting to those stimuli. For example, if gravity alone were considered, the hyphae organizing the pileus of mushrooms might be plagiotropic while forming the cap, those on the lower side becoming positively geotropic to organize the lamellae, while the hyphae organizing the hymenium would again be plagiotropic. Of course it is not supposed, and the experiments bear this out, that any case would yield to so simple an analysis as this, for it is still possible that the plant has within itself an inherited tendency toward a definite organization, and even if this is not admitted the common chemotropic and thigmotropic actions of the hyphae upon each other play an important part. That direct external stimuli also play an important part is shown by the non-development of *Lentinus lepideus*[7] in the dark. The caps of some species of Coprinus[8] also are dependent upon light

[6] ATKINSON, G. F., The development of *Agaricus campestris*. BOT. GAZETTE **42**:241–264. *pls. 6.* 1906; the older literature is reviewed here.

ALLEN, C. L., The development of some species of Hypholoma. Ann. Myc. **4**: 387–394. *pls. 3.* 1906.

[7] REINKE, J., Ueber Deformation von Pflanzen durch äussere Einflüsse. Bot. Zeit. **62**:81–112. *pl. 1.* 1904; see the literature given here.

BULLER, A. H. R., The reactions of the fruit-bodies of *Lentinus lepideus* Fr. to external stimuli. Annals of Botany **19**:427–438. *pl. 4.* 1905.

[8] BREFELD, O., Untersuchungen über Schimmelpilze **3**:87–97, 114–115. 1877.

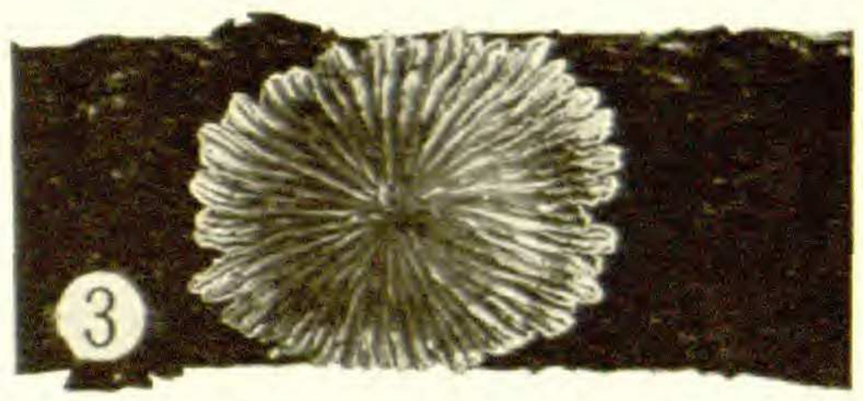
for their development. In these cases the development of the pileus is retarded or suppressed, so that it is probable that here light acts as something more than a tropic stimulus. BULLER (*l. c.*) has recently shown, however, that the lamellae of Lentinus develop first and most vigorously on the lower side of the young fruit-body when it arises obliquely from the substratum, and that this unilateral development is due to the effect of gravity. Here we have a change in form due to the effect of gravity. It is probable that the eccentricity of the stalks of tree- and stump-inhabiting forms is directly due to such action of gravity, for when some of these forms, like *Pleurotus ulmarius*, develop on the upper side of a fallen trunk they are symmetrical.

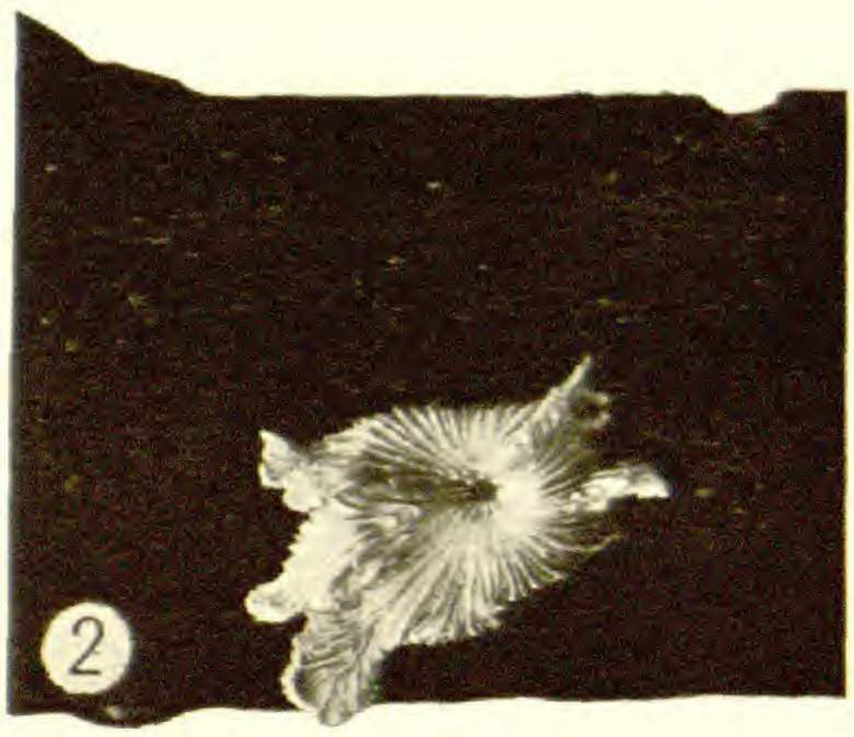
In *Polystictus cinnabarinus*, as in other shelf-forms, the fruit-bodies increase in size by growth at the margin. The hyphae near the lower side of the growing margin turn downward and produce the hymenophore. The epinastic growth (if this term, originally applied only to dorsiventral organs, may be employed) of these hyphae is due to their positive geotropism, for on the klinostat they grow uniformly in all directions. The organization of the hymenophore itself is not dependent upon gravity, for when this force is equalized all the hyphae form hymenial tissue. The differentiation of the fruit-body into an upper sterile and a lower fertile region is also due ultimately to the influence of gravity. All the hyphae are potentially fertile, but the development of a hymenium by the upper hyphae is inhibited finally by gravity. How this sterilization is brought about is another question. It is probable that the direct cause is to be sought in the mechanical or chemotropic influences of the hyphae upon each other. Since experiments were conducted both in light and in dark, it is evident that light is not a factor in this case.

The form of the more highly organized Schizophyllum is influenced in a less degree. It is evident that the general organization of the fungus is quite independent of the stimulus of gravity. There is one interesting phase, however, that needs to be considered. The fruit-bodies of this fungus are typically dorsiventral and laterally attached, yet on the klinostat they originate as small funnel-shaped bodies with the lamellae on the inside of the funnel; and when allowed to develop fully, the funnel expands and develops into a lobed disk,

stalked at the back and bearing the gills on the upper surface (*figs.* 1 and 2). It will be seen that the gills are not, as in all other Agaricaceae, on that surface of the pileus which is continuous with the stipe, *i. e.*, the lower surface, but on the opposite side, which corresponds to the dorsal surface of other mushrooms. In this respect Schizophyllum stands alone, at present, among the Agaricaceae. The growth of the fungus on the klinostat enables us to interpret the structure of the normal dorsiventral fruit-body.

The youngest primordia arise in the form of minute cups. If these are allowed to develop on the klinostat, the tendency of the pileus to develop equally on all portions shows itself. If, however, the fungus grows out more or less horizontally from the substratum, as it normally grows, the lower half of the pileus ceases to develop, while the upper half grows into a fan-shaped fruit-body. The pileus may be regarded as a funnel with the gills on the inside, having its lower half cut away and the upper half flattened out so as to expose the gills in their normal position toward the earth. The inhibition of growth of the lower half is ultimately due to gravity, since on the klinostat all portions develop equally. The same effect is produced when the fruit-bodies grow on the lower side of sticks, as they often do in nature. Such specimens expand symmetrically on the margin, producing a rotate fruit-body attached at the back





Schizophyllum commune. FIG. 1.—Stalked symmetrical fruit-body grown on the klinostat. FIG. 2.—Lateral view. FIG. 3.—Fruit-body developed on lower side of branch lying on the ground, showing symmetrical structure. × 1.

and with the lamellae radiating in all directions from the center (*fig. 3*).

In the highly differentiated Coprinus no formative influence of gravity could be observed. It is evident that here the organization of the fruit-body depends largely upon internal causes or upon stimuli not yet sufficiently analyzed.

In conclusion, it follows from the foregoing observations, on three widely separated forms of the Basidiomycetes, that although gravity has no apparent effect on the organization of the hymenophore,[9] it has a marked influence on determining the configuration of the fruit-body of some forms. This effect is most marked in the more primitive forms, which are thereby shown to be the more plastic. In the more highly differentiated forms this effect of gravity disappears. The effect of gravity on the configuration of Polystictus is due partly to the positive geotropic property of the hymenophore, and partly to the fact that the differentiation of the fruit-body into sterile and fertile tissue depends on the action of gravity. When this force is removed, the fruit-body assumes the resupinate or a pulvinate form characteristic of the simplest types of the Basidiomycetes.

THE UNIVERSITY OF CHICAGO

[9] This term applies only to the parts immediately bearing the hymenium, *i. e.*, the gills, spines, etc., and not, as it is sometimes used, to the whole fruit-body.